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Comparison of Herbicides for Reducing Annual Grass Emergence in Two Great Basin Soils

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Abstract

Reducing seed germination and seedling emergence of downy brome (*Bromus tectorum* L.) improves the success of revegetating degraded shrubland ecosystems. While pre-emergence herbicides can potentially reduce these two processes, their impact on germination and emergence of downy brome and revegetation species in semiarid ecosystems is poorly understood and has not been comprehensively studied in soils with potentially contrasting herbicide bioavailability (i.e., residual plant activity). We designed a greenhouse experiment to evaluate the effects two pre-emergence acetolactate synthase–inhibiting herbicides (rimsulfuron and imazapic) on germination and emergence of downy brome and two revegetation grass species (crested wheatgrass [*Agropyron cristatum* {L.} Gaertn.] and bottlebrush squirreltail [*Elymus elymoides* {Raf.} Swezey]) that were grown in representative soils from salt desert and sagebrush shrublands. Pre-emergence herbicides significantly ($P < 0.05$) reduced seedling emergence and biomass production of downy brome and crested wheatgrass and increased mortality more so in sagebrush compared to salt desert soil, suggesting that these common Great Basin soils fundamentally differ in herbicide bioavailability. Also, germination and emergence of the two highly responsive species (crested wheatgrass and downy brome) were clearly more impacted by rimsulfuron than imazapic. We discuss these results in terms of how the specific soil physiochemical properties influence herbicide adsorption and leaching. Our results shed new light on the relative performance of these two promising herbicides and the importance of considering soil properties when applying pre-emergence herbicides to reduce germination and emergence of invasive annual grasses and create suitable seedbed conditions for revegetation.

Resumen

Reduciendo la germinación y emergencia del pasto bromo velludo (*Bromus tectorum* L.) mejora las practicas de re-vegetación en los ecosistemas de matorral degradados. Mientras que los herbicidas de pre-emergencia puede potencialmente reducir estos dos procesos, sus impactos en germinación y emergencia en pasto bromo velludo y re-vegetación de especies en ecosistemas semi áridos no está bien entendido y no ha habido estudios profundos en suelos con potencial de contrastar la bio-disponibilidad del herbicida por ejemplo en la actividad residual en la planta. Se diseño un experimento en invernadero para evaluar el efecto de pre-emergencia de acetolactate inhibidor de herbicida (rimsulfuron e imazapic) en la germinación y emergencia del bromo velludo y dos especies de pasto para re-vegetación (triguillo crestado [*Agropyroncristatum* {L.} Gaertn.] y escobilla cola de ardilla [Elymuselymoides {Raf.}Swezey]) los cuales fueron sembrados en suelos representativos de desierto salado y matorrales de artemisa. El herbicida de pre-emergencia reduce ($P < 0.05$) significativamente la emergencia de plántulas y producción de biomasa de bromo velludo y triguillo crestado y aumenta mas la mortalidad en artemisa comparado con el suelo salino del desierto, sugiriendo que estos suelos típicos del Great Basin difieren bastante en bio-disponibilidad del herbicida. Además, la germinación y emergencia de las dos especies altamente responsables (triguillo crestado y bromo velludo) fue más impactado por el rimsulfuron que el imazapic. Discutimos estos resultados en términos de cómo las propiedades fisicoquímicas del suelo influyen en la absorción del herbicida y escurrimiento. Nuestros resultados ofrecen nuevos senderos con respecto al desempeño de estos dos prometedores herbicidas y la importancia de considerar las propiedades del suelo cuando se vayan a hacer aplicaciones de herbicidas pre-emergentes para reducir la germinación y emergencia de pastos anuales invasores y crear un banco de siembra adecuado para la re-vegetación.

Key Words: bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), downy brome (*Bromus tectorum* L.), pre-emergence herbicides, salt desert and sagebrush shrubland, soil organic matter

INTRODUCTION

Invasive annual grasses have the potential to seriously impact ecosystem processes in semiarid regions, resulting in altered structure and function that favor their continued dominance (Ehrenfeld et al. 2005). Moreover, the long-term effects of annual grass invasion are predicted to increase with time since invasion, depending on their functional distinctiveness and abundance within the ecosystem (Strayer et al. 2006).

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Incidentally, both functional distinctiveness and abundance of invasive grasses increase as perennial plant functional types decline with frequent wildfires fueled by high annual grass productivity (D'Antonio and Vitousek 1992; Brooks et al. 2004). Annual grass abundance is reinforced not only by altered ecosystem structure, function, and disturbance regimes but also by a suite of dispersal and reproductive traits that perpetuate their persistence (Sakai et al. 2001; Funk 2008; Moles et al. 2008). Identifying methodologies to target these traits and their influence on key ecosystem processes may present an ecologically based approach to reduce the abundance of invasive annual grasses and improve revegetation success (Sheley et al. 2010).

Annual grasses persist within disturbed ecosystems by exhibiting numerous plant traits that are functionally distinct from resident native species. First, compared to perennial species, they have a shorter life span and earlier emergence, which enhance growth potential, competitive dominance, and seed production (Sutherland 2004; Verdu and Traveset 2005). Second, higher growth rate and earlier maturity enable them to more favorably respond to anthropogenic disturbance than perennial species (Corbin and D'Antonio 2004; HilleRisLambers et al. 2010) and rapidly exploit soil resources when they are most available (Garnier 1992; Seabloom et al. 2003; James et al. 2009). Combined, these traits provide mechanisms for annual plants to create three restoration obstacles: 1) persistent seedbanks (Marañón 1998; Facelli et al. 2005), 2) continued dominance of annual species during community assembly (Grman and Suding 2010; James et al. 2011), and 3) an intensely competitive environment for both resident and artificially seeded species during revegetation (Eliason and Allen 1997; Hamilton et al. 1999; Humphrey and Schupp 2001, 2004). Addressing these obstacles by "minimizing deposits and maximizing withdrawals" (Menalled and Schonbeck 2011) from seedbanks is thus a necessary precursor to reduce interference on seeded species during revegetation (Forcella et al. 1993; Eiswerth et al. 2009).

Numerous measures can be used during the life cycle of annual grasses to influence seedbanks by reducing seed production and preventing seeds from germinating. These include early-spring targeted grazing to reduce productivity and seed production (Harmoney 2007), summer prescribed burns to consume abundant litter and seeds in leaf litter (Diamond et al. 2009; Pyke et al. 2010), and pre-emergence application of pathogens and herbicides to kill seeds and emerging plants (DiTomaso et al. 2010; Meyer et al. 2010). Herbicides can be particularly important because if viable seeds survive to germinate and emerge, annual grasses can quickly regain dominance and directly interfere with revegetation efforts (Evans et al. 1969; Morris et al. 2009; Davies 2010).

Because pre-emergence herbicides are designed to be bioavailable within soils (capable of influencing life functions of plants), many interactive factors influence their capacity to reduce germination and emergence of annual grasses. For example, soil bioavailability of acetolactate synthase (ALS)–inhibiting herbicides (e.g., sulfonylureas and imidazolinones) is strongly influenced by their organic/molecular structure and adsorption/desorption to minerals and organic matter, degradation by soil microorganisms, chemical hydrolysis, and dissipation and/or leaching from soil (Goetz et al. 1990; Loux and Reese 1993; Schneiders et al. 1993; Vicari et al. 1996; Dinelli et al. 1997). The complexity of soil bioavailability is further compounded when considering differential herbicide injury to target weeds and nontarget revegetation species (Obrigawitch et al. 1998; Hollaway et al. 2006). Consequently, identifying the underlying plant traits responsible for pre-emergence herbicide injury and clarifying how differences in soil physiochemical properties influence seed germination and emergence of invasive annual grasses will improve weed control and prevent unnecessary injury to revegetation species. Unfortunately, these processes have not been studied extensively for semiarid rangeland ecosystems, where pre-emergence herbicide use is currently a major component of integrated weed management and revegetation on lands impacted by invasive annual grasses (Monson 2004; DiTomaso et al. 2010).

Salt desert and sagebrush shrublands of the Great Basin (western United States) are currently suffering from the impacts of annual grasses and the possibility of future expansion within the region (West 1988; Young and Longland 1996; Young and Allen 1997; Bradley 2010). In particular, dominance of the invasive annual grass downy brome (*Bromus tectorum* L.) has increased fire frequency and the widespread loss of native species (D'Antonio and Vitousek 1992; Brooks et al. 2004). Efforts to reduce downy brome dominance with integrated management prior to revegetation has had poor success across these shrublands (Robocker et al. 1976; Eiswerth et al. 2009), which differ in many characteristics, including elevation, precipitation, topography, vegetation, soils, and disturbance history (Knapp 1996; West 1983a, 1983b; West 1988). Thus, greater understanding of how downy brome and revegetation species respond to pre-emergence herbicide applications in contrasting Great Basin soils may improve the integrated management of invasive annual grasses in this critical region.

We designed a greenhouse experiment to evaluate the effects of two pre-emergence ALS herbicides on germination and emergence of downy brome and two revegetation grass species grown in representative soils from salt desert and sagebrush shrublands that potentially vary widely in herbicide soil bioavailability. Because sagebrush soils typically have higher soil organic matter, lower soil pH, and higher clay content and cation exchange capacity, we hypothesized that seed germination, seedling emergence, and seedling mortality of downy brome and perennial revegetation grasses would be reduced more by pre-emergence herbicides in sagebrush than salt desert soils. In addition, we anticipated that a detailed analysis of germination and emergence would provide new insights into how application of pre-emergence herbicides to these soils influences downy brome injury and the performance of desirable perennial grasses. Clarifying these currently unknown factors may lead to improved herbicide applications and revegetation success for downy brome–dominated shrublands and other regions experiencing similar annual grass invasions.

MATERIALS AND METHODS

Soils for a greenhouse study were obtained in May 2010 from two downy brome–dominated ecological sites in western Box Elder County, Utah, near the town of Park Valley. These two semidesert ecological sites are broadly distributed in Major

Land Resource Area 28A (Great Salt Lake Area) and throughout the Great Basin (US Department of Agriculture, Natural Resources Conservation Service [USDA, NRCS] 2011). Climate of this region is characterized by cold snowy winters and hot dry summers with most of the precipitation occurring through snow and spring rains ranging from 200 to 300 mm per year. Mean annual air temperature is 10°C. Parent material is derived from alluvium, originating from the canyons of the Raft River Mountains to the north (Center for Environmental Informatics [CEI] 2011).

The first ecological site is classified as semidesert alkali loam (black greasewood [*Sarcobatus vermiculatus* {Hook} Torr.]; lat 41°45′25.64″N, long 113°16′6.46″W). Soils are in the Kunzler series, classified as coarse-loamy mixed, superactive, mesic, durinodic Xeric Haplocalcids, and occur on over 100 000 ha in the Great Basin (CEI 2011). This site occurred at 1 545-m elevation on 2% slope and a south aspect. Vegetation of this salt desert ecosystem is typically dominated by the shrubs black greasewood, Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* [Beetle & Young] S.L. Welsh), and rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird subsp. *consimilis* [Greene] G.L. Nesom & Baird). The herbaceous understory is composed of Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth) and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey; West 1983a, 1983b). The second ecological site is classified as semidesert gravelly loam (Wyoming big sagebrush; lat 41°49′26.21″N, long 113°17′25.21″W). Soils are in the Kapod and Donnardo series, classified as loamy-skeletal, mixed, superactive, mesic Calcic Argixerolls and loamy-skeletal, mixed, superactive, mesic Typic Argixerolls, which occur on over 40 000 ha in the Great Basin (CEI 2011). This site occurred at 1 680-m elevation on 3% slope and a south aspect. Wyoming big sagebrush and other native herbaceous grasses like bluebunch wheatgrass (*Pseudoregneria spicata* [Pursh] A. Löve) and bottlebrush squirreltail typically dominate this sagebrush ecosystem. At both sites, soils were excavated to a 15-cm depth from a 2-m^2 area, sifted through a 1.25-cm^2 sieve in the field to remove debris and rocks, and thoroughly mixed.

Experimental Design

In the laboratory, 15 2-kg soil subsamples from each ecological site were air-dried at 25°C for 14 d, passed through a 2-mm sieve to further remove debris and gravel, and hand ground with a mortar and pestle. Soil texture was determined using the hydrometer method to quantify percentage sand, silt, and clay (Gee and Bauder 1986). Samples (40 g) were mixed with a 100-mL sodium hexametaphosphate–water solution and 250 mL of deionized water and shaken at 150 rpm for 1 h, placed into a 1-L cylinder, and filled with deionized water. A custom plunger was used to mix the slurry before measuring its temperature and density ($g \cdot L^{-1}$) with a Bouyoucos hydrometer (14-331-5C; Thermo Scientific, Beverly, MA) after 30 s and 1 440 min. These two variables were used to determine percent sand, silt, and clay content. Soil pH was measured by mixing 15 g of soil with 30 mL of deionized water, shaking at 100 rpm for 30 min, and then measuring the slurry with a pH meter (Orion 3 star bench-top pH meter; Thermo Scientific; Thomas 1996). Total N and C were determined on 0.1 g of soil combusted with a LECO CHN 2000 Autoanalyzer (Leco Corp, St Joseph, MI; Wolf et al. 1994). Electrical conductivity was determined on 50 g of soil mixed with 50 mL of deionized water, shaken at 200 rpm for 2 h, and filtered through a filter paper (Grade 4; Whatman International Ltd, Maidstone, England) using a vacuum system. Electrical conductivity was measured on the filtered solution with an ionic probe (Orion 3 star bench-top conductivity meter, Thermo Scientific; Rhodes 1996). Cation exchange capacity (CEC) and organic matter content (OM) were analyzed by the Utah State University Analytical Laboratory using the NaOAc/NH_4OAc replacement method for CEC and the loss on ignition/ash method for OM ($n = 5$).

Soil from each ecological site was placed in 720-plastic containers (0.3-L volume; 4 cm diameter × 20 cm height) with 5 × 5 cm paper towel placed in the bottom of each container to allow water drainage and prevent the loss of soil. For each soil, 240 containers were planted at a rate of four seeds per container with one of the three following plant species: the invasive annual grass downy brome, the exotic perennial grass crested wheatgrass (*Agropyron cristatum*, cultivar Hycrest), and the native perennial grass bottlebrush squirreltail (Rattlesnake germplasm). Certified perennial grass seed was obtained from a commercial source, while downy brome seed was collected from Box Elder County, Utah (Johnson Canyon; lat 41°53′32.61″N, long 112°12′55.53″W). An unreplicated germination test in these soils indicated that seed viability of downy brome was similar to viability of the certified seed sources (50% and 60%). Seeds were hand cleaned and selected for the experiment based on uniformity in size. Planting included placing four seeds of an individual species concentrically near the center of each container, covering with 5 mm of soil, and watering daily to initiate germination.

Four containers of each species were nested within each soil type within a rack, and individual container racks were randomly assigned to one of the six possible combinations of herbicide treatment (deionized water control, imazapic, and rimsulfuron) and application rate (70 or 105 g active ingredient $\cdot$ ha^{-1}). A rack from each of the six treatments was placed into a randomized complete block configuration on a greenhouse bench with nine replicates; total racks equaled 54. Prior to seedling emergence, herbicide treatments were applied in an enclosed spray chamber connected to an onboard control (E-410; Control Assemblies Co, Minneapolis, MN). Herbicide treatments were independently mixed and applied to replicate container racks. Spray was applied with an even-flat-fan nozzle (Teejet 8002; Spraying Systems Co, Wheaton, IL) calibrated to cover a 66-cm band at 76 cm $\cdot$ s^{-1} at 105 kPa. The spray nozzle remained on a chain-driven path 40 cm above the soil surface. Numerous calibration trials were performed by spraying absorbent sheets of paper with deionized water and quickly weighing to determine application rate. The untreated control was applied in the same manner, except with deionized water. To avoid contamination between treatment applications, the sprayer was rinsed with deionized water, and the spray chamber was thoroughly washed. After herbicide treatments were applied, racks were returned to the greenhouse, and plants were grown for an additional 27 d after treatment (DAT). Greenhouse temperature was maintained at 30°C during the day and 15°C at night with the aid of a greenhouse cooling system. No supplemental lighting was used, and the day length was roughly 16 h during the experiment. Each day individual containers were supplied with 15 mL of deionized water, avoiding the possibility of any water drainage, while adequately hydrating the entire soil. The 16 potential seedlings of each species within a container rack were considered an experimental unit.

Percentage seedling emergence was recorded throughout the experiment every other day (no adjustments were made for differences in seed viability). Shoot and roots were harvested at 27 DAT by emptying containers on a 2-mm screen, lightly washing soil from roots, and excising roots from shoots with a razor blade. Shoots and roots were combined into experimental units and placed in a convective oven at 60°C for 48 h to determine dry mass. Percentage seedling mortality was calculated from the difference between maximum emergence, which was achieved on different dates for species and final seedling emergence.

Statistical Analysis

Soil-property data from the salt desert and sagebrush sites were compared with Student's *t* test. The randomized complete block design greenhouse study was analyzed as a factorial experiment with soil type, herbicide treatment, herbicide rate, and grass species as main effects. For each date, we calculated mean percentage seedling emergence as opposed to cumulative percentages, so it is clear to determine when seedling mortality was occurring. Final percentage seedling emergence at 27 DAT, percentage seedling mortality, and final dry mass of roots and shoots were analyzed with an analysis of variance (ANOVA; general linear) model. Significant effects were further analyzed with Tukey's HSD mean separation procedure. Box–Cox transformations were performed on data as needed to improve normality and meet the assumptions of ANOVA. All analyses were performed with $\alpha = 0.05$ using JMP 8 (SAS Institute, Cary, NC).

RESULTS

The salt desert soil had significantly lower organic matter content, CEC, and percentages of clay and sand compared to the sagebrush soil (Table 1). In contrast, the salt desert soil had significantly greater soil pH, EC, and percentage of silt than the sagebrush soil.

Table 1. Results of physiochemical soil analysis of salt desert shrub and sagebrush ecological sites. Values are means ($n = 15$, except $n = 5$ for organic matter and cation exchange capacity; ± 1 SE). All measures were significantly different between soils based on *t* tests ($P < 0.05$).

Soil measure	Salt desert	Sagebrush
Organic matter (%)	1.80 (0.05)	3.78 (0.13)
Cation exchange capacity ($cmol \cdot kg^{-1}$)	15.88 (0.07)	19.62 (0.15)
pH	9.53 (0.01)	7.91 (0.01)
Electrical conductivity ($dS \cdot m^{-1}$)	0.352 (0.004)	0.257 (0.003)
Sand (%)	60.4 (0.3)	65.6 (0.3)
Silt (%)	30.6 (0.3)	23.3 (0.3)
Clay (%)	9.0 (0.1)	11.1 (0.1)

Neither the main effect of herbicide rate nor any interactions with herbicide rate significantly influenced any of the experimental variables. Consequently, data for the two rates were combined and reanalyzed with reduced models (Table 2).

Seedling emergence was generally greater in the sagebrush soil than the salt desert soil, and crested wheatgrass and downy brome had similar emergence within a soil type (Table 2; Fig. 1). In contrast, seedling emergence of squirreltail was clearly lower than the other two grasses but more so in the salt desert soil. While imazapic and rimsulfuron had similar effects on seedling emergence patterns relative to the control in both soil types, seedling emergence in the rimsulfuron treatment was always significantly lower than the control, and the reduction by day 27 was threefold in the sagebrush soil and onefold in the salt desert soil (Table 2; Fig. 2). Likewise, imazapic and the control had similar effects on seedling emergence of all three grasses; however, the reduction caused by rimsulfuron was significant for crested wheatgrass and downy brome but not squirreltail (Table 2; Fig. 3).

Seedling mortality was contingent on how treatment and species interacted with shrubland soil types (Table 2). While herbicide treatments did not greatly influence mortality in the salt desert soil, both herbicide treatments significantly increased seedling mortality when applied to the sagebrush soil (Fig. 4A). Correspondingly, mortality was generally highest in the sagebrush soil, yet the difference between soil types was significant only for crested wheatgrass (Fig. 4B).

Treatment effects on shoot dry mass depended on significant interactions with both soil type and species (Table 2). Relative to the control, both herbicide treatments significantly reduced shoot dry mass in both soils; however, rimsulfuron reduced shoot dry mass significantly more than imazapic in the sagebrush soil type (Fig. 5A). Similarly, both herbicides significantly reduced shoot dry mass of crested wheatgrass and downy brome but not squirreltail (Fig. 5B). Rimsulfuron reduced shoot dry mass more than imazapic for downy brome but not for crested wheatgrass and squirreltail.

Soil type interacted with both treatment and species for root dry mass (Table 2). Both herbicides significantly reduced root dry mass relative to controls in both soils; however, imazapic showed greater reduction in the salt desert soil (Fig. 6A). Root dry mass of squirreltail was also significantly lower than the other grasses only in the salt desert soil type (Fig. 6B).

DISCUSSION

Reducing seed germination and emergence of invasive annual species greatly improves the success of seeding desirable seeded species (DiTomaso 2000; Wisdom and Chambers 2009; Davies and Sheley 2011). However, directly targeting these two critical processes with pre-emergence herbicides has been unpredictable in semiarid rangeland soils (Monaco et al. 2005; Kyser et al. 2007; Morris et al. 2009), possibly because of differences in residual soil bioavailability. Our observation that both pre-emergence herbicides reduced seedling emergence and biomass production yet increased mortality more so in sagebrush compared to salt desert soil supports our hypothesis and clarifies how these two common

Table 2. Analysis of final seedling emergence, seedling mortality, and dry mass of shoots and roots from ANOVA. Significant effects with bolded *P* values are emphasized in the Results section.

		Final percentage seedling emergence		Percentage seedling mortality		Shoot dry mass		Root dry mass	
Effect	df	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Treatment (Trt)	2	43.21	< .0001	13.54	< .0001	48.72	< .0001	164.20	< .0001
Soil type (ST)	1	62.71	< .0001	7.48	0.0067	28.07	< .0001	2.17	0.1422
Species (Spp)	2	46.35	< .0001	1.40	0.2496	19.40	< .0001	7.40	0.0008
Trt × ST	2	7.87	**0.0005**	6.66	**0.0015**	11.48	**< .0001**	31.36	**< .0001**
Trt × Spp	4	7.26	**< .0001**	1.74	0.1414	3.48	**0.0089**	1.27	0.2834
ST × Spp	2	6.43	**0.0019**	4.69	**0.0100**	1.55	0.2149	4.14	**0.0172**
Trt × ST × Spp	4	1.40	0.2335	2.27	0.0627	0.39	0.8178	1.16	0.3316

Great Basin soils fundamentally differ in herbicide bioavailability. Consequently, we propose that physiochemical properties of these two soils may influence herbicide adsorption and subsequent leaching. Furthermore, because germination and emergence were clearly more impacted by rimsulfuron than imazapic, we present a detailed assessment of how two critical observations shed new light on the relative performance of these two promising herbicides, namely, 1) delayed injury in crested wheatgrass seedling emergence in the imazapic treatment and 2) no reduction in downy brome seedling emergence in the imazapic treatment.

Because this was a controlled experiment, significantly greater herbicide impacts on seedling emergence, mortality, and growth in sagebrush soil relative to the salt desert soil appears to be a consequence of the former soil having greater herbicide bioavailability. In general, soil adsorption, soil stability, and plant injury for pre-emergence herbicides strongly depend on soil colloidal properties, including organic matter content, clay content, and soil CEC (Morrica et al. 2000; Pusino et al. 2004; Monquero et al. 2008), which were notably higher in the sagebrush soil. Lesser impact of both herbicides on seedling shoot and root growth in the salt desert soil further emphasizes how lower herbicide adsorption relative to the sagebrush soil likely reduced bioavailability in our experiment. Bioavailability is also dependent on chemical hydrolysis and leaching because chemicals that hydrolyze more readily are subject to leaching and poor adsorption to soils. For example, rimsulfuron hydrolysis, resulting in contraction of the sulfonylurea bridge, takes place rapidly in distilled water (half-life = 2.2 d), is instantaneous in alkaline solutions above soil pH of 8, and accelerates at temperatures greater than 25°C (Schneiders et al. 1993; Dinelli et al. 1997; Martins and Mermoud 1999; Scrano et al. 1999). In addition to hydrolysis in aqueous solutions, soil pH also strongly influences adsorption and hydrolysis in soils. For example, adsorption of the sulfonylurea herbicide azimsulfuron was negatively correlated with soil pH (Pusino et al. 2004), and rimsulfuron hydrolysis was found to increase above pH of 7 in six Colorado soils (Vicari et al. 1996). Although less is known about imazapic bioavailability in soils, photolysis in aqueous solutions similarly increases with solution pH and temperature up to 40°C, and the rate of photolysis will plateau above pH of 5 (Harir et al. 2007). In soils, the adsorption of imazapic also decreases with increasing pH as the H^+ ion dissociates from the carboxylic group on the imidazolinone ring, making the molecule predominantly negatively charged and more susceptible to leaching (Inoue et al. 2007, 2009). Furthermore, even in clay soils, heavy simulated precipitation of 90 mm led to deep percolation of imazapic and poor weed control in superficial soil layers in sugarcane fields (Hernandez et al. 2001). In light of our experiment, lower herbicide adsorption and higher subsequent leaching in the salt desert soil thus appears to be a plausible mechanism responsible for the overall lower herbicide

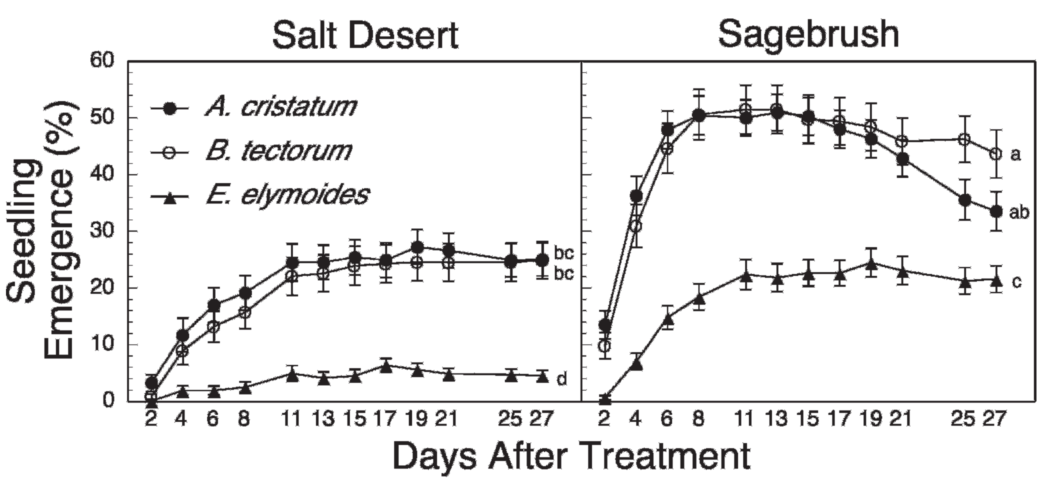

Figure 1. Mean (± 1 SE) percentage seedling emergence of three grass species grown in different shrubland soil types (combined herbicide treatments). Different lowercase letters indicate significant ($P < 0.05$) differences 27 d after pre-emergence herbicide application.

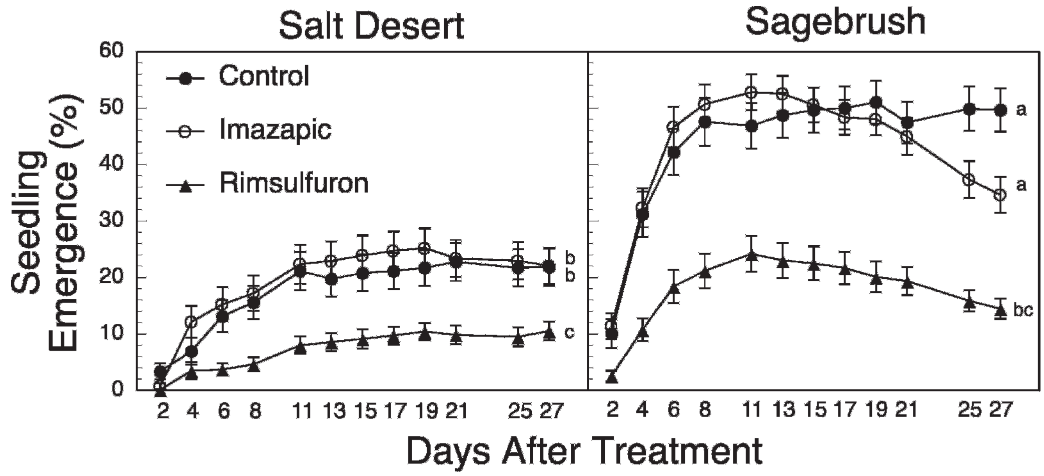

Figure 2. Mean (± 1 SE) percentage seedling emergence in different shrubland soil types following application of three herbicide treatments (combined grass species). Different lowercase letters indicate significant ($P < 0.05$) differences 27 d after pre-emergence herbicide application.

effect in our experiment, especially because ample water was applied to facilitate degradation and leaching within containers, soil pH was higher in the salt desert soil, and greenhouse temperatures exceeded 25°C each day.

The unique manner in which crested wheatgrass responded in our experiment provides a potential mechanism of how herbicide bioavailability varies between the two Great Basin soils we evaluated. Seedling emergence remained stable in the salt desert soil but declined in both treatments after day 11 in the sagebrush soil relative to the control, causing significant increases in mortality, primarily in crested wheatgrass (Figs. 2, 4A, and 3, respectively). This distinct pattern suggests that both herbicides may have experienced greater initial adsorption and subsequently lower leaching in the sagebrush soil, making crested wheatgrass more susceptible to injury. Greater initial adsorption in the sagebrush soil also likely provided more residual herbicide, prolonging the exposure of emerged crested wheatgrass seedlings. Lower adsorption and subsequent leaching in the coarse-loamy salt desert soil would likewise have a diminished effect by exposing seedlings to less herbicide, given its lower organic matter, lower CEC, and higher pH. Similar to our study, when rimsulfuron and two other sulfonlyurea herbicides were applied to bare soil with adequate adsorption potential, leaching was nearly undetectable, even under heavy irrigation in Canadian prairie soils (Cessna et al. 2010). Similarly, imazapic experienced greater adsorption (lower dissipation time) in a clay soil than a sandy loam in Brazil (Ulbrich et al. 2005).

Our observation of no reduction in downy brome seedling emergence in the imazapic treatment was the most surprising result of our experiment. The question essentially becomes, why was downy brome emergence not reduced by imazapic even though this herbicide significantly reduced combined species mortality and drastically reduced shoot and root growth of this invasive annual grass? Although both herbicides were applied at the same active ingredient rates, it is possible that they fundamentally differ in plant uptake mechanisms and disruption of the ALS enzyme; however, neither of these factors was evaluated in our study (but see Stidham 1991; Tranel and Wright 2009). Another reason why imazapic did not reduce downy brome emergence may be the relative performance of pre-emergence herbicides, which typically differ in water solubility and extent of adsorption in soils (Singh et al. 1990; Barriuso et al. 1992). While direct comparisons of soil mobility and susceptibility to leaching between rimsulfuron and imazapic have not been made, our appraisal of independent

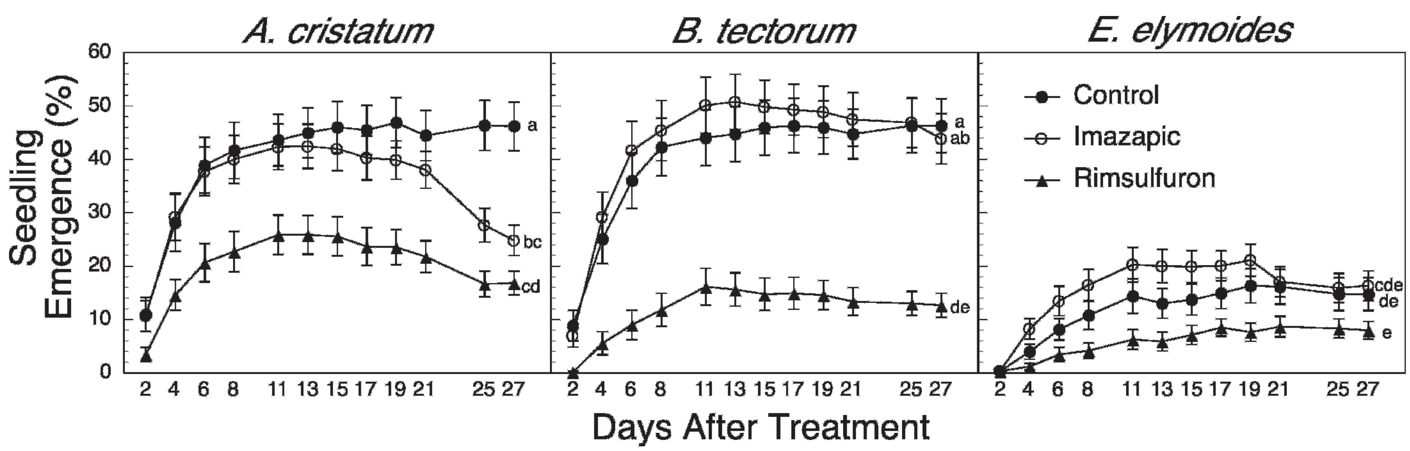

Figure 3. Mean (± 1 SE) percentage seedling emergence of three grass species following application of three herbicide treatments (combined shrubland soil types). Different lowercase letters indicate significant ($P < 0.05$) differences 27 d after pre-emergence herbicide application.

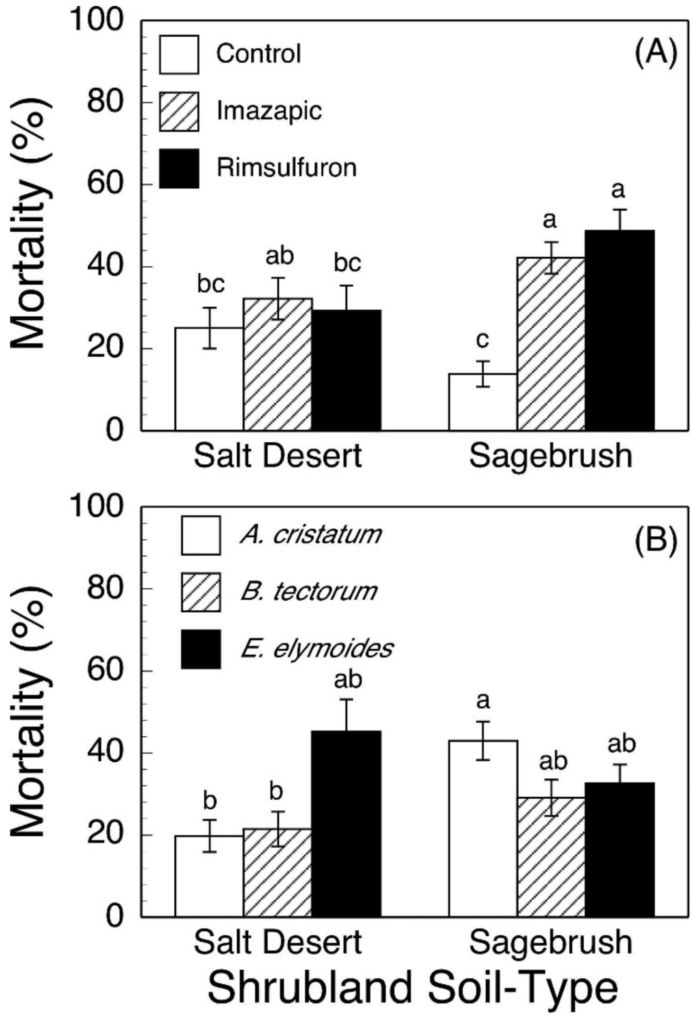

Figure 4. Mean (± 1 SE) percentage seedling mortality in different shrubland soil types following application of three herbicide treatments (**A**, combined grass species) and for three grass species (**B**, combined herbicide treatments). Different lowercase letters indicate significant ($P < 0.05$) differences 27 d after pre-emergence herbicide application.

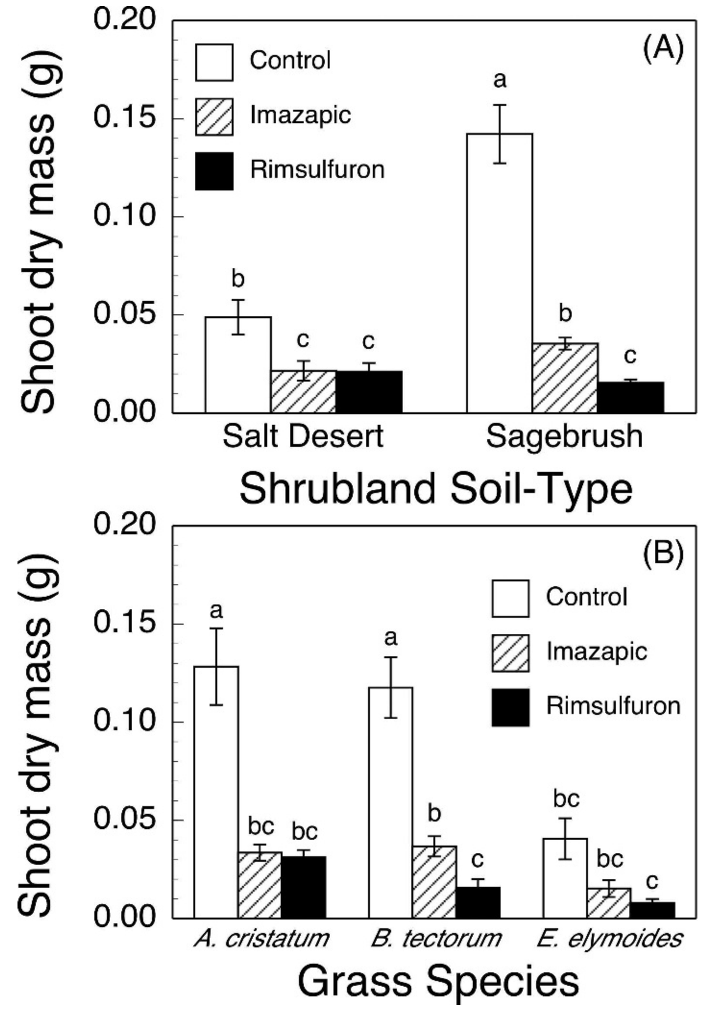

Figure 5. Mean (± 1 SE) shoot dry mass following application of three herbicide treatments to different shrubland soil types (**A**, combined grass species) and for three grass species (**B**, combined shrubland soil types). Different lowercase letters indicate significant ($P < 0.05$) differences 27 d after pre-emergence herbicide application.

studies is that leaching potential in soils is much greater for imazapic than rimsulfuron (Schneiders et al. 1993; Inoue et al. 2007, 2009; Cessna et al. 2010). These relative differences between imazapic and rimsulfuron not only are consistent with our interpretation of lower residual bioavailability in the salt desert soil but also indicate the possibility that imazapic may have dissociated and leached within growth containers. Consequently, the combined effects of frequent watering and herbicide percolation may be responsible for 1) downy brome emergence not being significantly different between the control and imazapic treatment and 2) the delayed imazapic effect in crested wheatgrass. Furthermore, we suggest that only after roots elongated deeper into the soil were seedlings exposed to imazapic and growth subsequently impaired. Finally, because imazapic did not reduce downy brome emergence and roots likely developed until they were exposed to imazapic, shoots were capable of achieving twofold greater productivity than in the rimsulfuron treatment.

Lower herbicide injury to bottlebrush squirreltail than the highly responsive species—crested wheatgrass and downy brome—is not clearly explained by the responses we measured. It is likely that fourfold lower emergence of bottlebrush squirreltail in salt desert compared to sagebrush soil limited our ability to detect significant herbicide or herbicide-by-species interactions. Although neither of the two herbicides we evaluated reduced any of the measured bottlebrush squirreltail variables, general patterns for mortality and shoot dry mass were similar to the responsive species. Consequently, we are reluctant to infer that bottlebrush squirreltail responds fundamentally differently than the other grasses to these pre-emergence herbicides. Our position is supported by other studies that showed significant bottlebrush squirreltial injury from imazapic and other sulfonylurea herbicides (Monaco and Creech 2004; Sheley et al. 2007).

IMPLICATIONS

Principles linking ecological processes with invasive plant management are beginning to emerge for semiarid rangeland ecosystems (James et al. 2010). For example, failing to directly

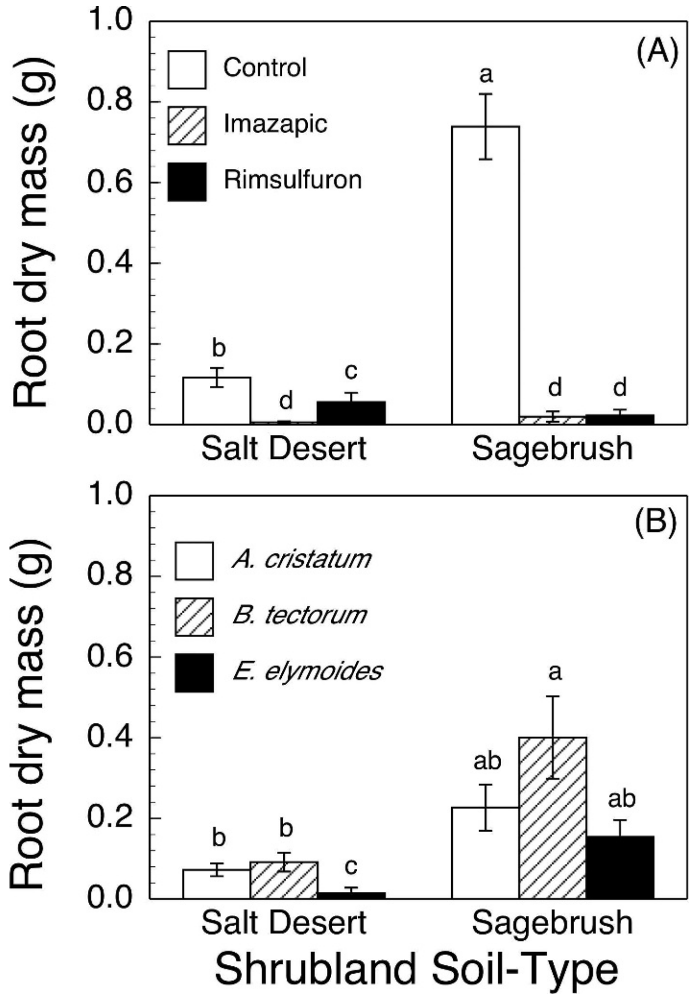

Figure 6. Mean ($\pm$ 1 SE) root dry mass in different shrubland soil types following application of three herbicide treatments (**A,** combined grass species) and for three grass species (**B,** combined herbicide treatments). Different lowercase letters indicate significant ($P < 0.05$) differences 27 d after pre-emergence herbicide application.

target invasive annual grass seed production, seedbanks, and seedling emergence can seriously hamper revegetation potential of a given site (Rafferty and Young 2002; Morris et al. 2009). Herein, we show that the capacity of select pre-emergence herbicides to target seedling germination and emergence is strongly dependent on soil properties. Although this dependence is limited to the specific soils, herbicides, and seed sources we evaluated, our data suggest a number of implications to consider when using these herbicides to reduce invasive annual grass emergence and minimize nontarget effects on revegetation species. First, our results suggest that differences in residual herbicide bioavailability is a plausible mechanism for why initial control of annual grasses and injury to seeded revegetation species was found to be greater in sagebrush soils vs. salt desert soils (Morris et al. 2009). Given the broad variation in soil texture and organic matter within and between semiarid rangeland ecosystems, responses to pre-emergence herbicides may vary widely from site to site because of differences in soil herbicide bioavailability. These differences should be anticipated prior to selecting revegetation species and applying pre-emergence herbicides. Second, delayed plant injury and the potential differences we observed in herbicide adsorption and leaching emphasize the importance of following herbicide label instructions and properly timing herbicide applications to avoid periods of high rainfall in semiarid rangelands. This may necessitate applying pre-emergence herbicides in the summer to improve herbicide bioavailability prior to potential annual grass germination and emergence associated with autumn precipitation and to minimize injury to revegetation species, which increases as the time between application and seeding decreases (Sbatella et al. 2011). Finally, because herbicide efficacy depends on bioavailability in soils, we concur with previous suggestions that removing obstructive litter or vegetation from the soil surface with management activities will greatly enhance soil adsorption and the effectiveness of pre-emergence herbicides (Monaco et al. 2005; Kyser et al. 2007; Davies 2010).

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